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Climate, ecology, and the spread of herding in eastern Africa

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ABSTRACT

The spread of early herders across Africa is a pivotal event in prehistory, but the context of this event remains poorly understood due to a lack of paleoenvironmental data. We present new radiocarbon dates and multi-proxy Holocene paleoecological records for two distinct settings on the pathways through which livestock herding spread across eastern Africa: the Lake Turkana Basin, which has the earliest record of livestock in eastern Africa, and the Lake Victoria Basin, located farther south. Herbivore diet as inferred from tooth enamel carbon isotopes (n = 368), and pollen and leaf wax biomarker data, do not support a uniform ecological response to increased aridity at the end of the African Humid Period ~5 kya, as had been previously thought. Rather, climate change had basin-specific ecological effects, and these in turn met differing human responses. Rather than extrapolating local ecological effects from regional climate records, archaeologists require basin-specific paleoecological data, deeply integrated with archaeological findings. This paper provides such integration for the first time in eastern Africa. Our results highlight the climatologically and ecologically distinctive areas around lake margins, necessitating future paleoenvironmental and archaeological research in inland areas.

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1. Introduction

Much attention has been given to understanding the processes governing ecological change in eastern Africa over geologic time, and how such change is reflected in the archaeological record (Potts, 2013; deMenocal, 2013). These discussions have focused on the role of orbital forcing (Claussen et al., 1999; deMenocal et al., 2000) in shaping ecosystem structure over time (deMenocal, 2011; Magill et al., 2013a), and the relationship between solar insolation and the abundance of C_3 (woody trees, shrubs, and forbs) vs. C_4 (lowland tropical grasses) plants. Paleoecologists employ proxies such as pollen, leaf wax biomarkers, and stable isotopes in herbivore tooth enamel and soil carbonates to create paleoenvironmental reconstructions, but these proxies are rarely analyzed in conjunction with one another in terrestrial environments (Levin, 2015).

African climate is primarily driven by the precession of the equinoxes, which dictates the location and convective strength of the intertropical convergence zone (ITCZ) (Kutzbach, 1981; Berger and Loutre, 1997; Battisti and Naylor, 2009) (Appendix Figure A.1). The ITCZ moves seasonally across the equator, influencing seasonal rainfall due to differential heating between land and sea. When Northern Hemisphere peak solar insolation occurs, the ITCZ strengthens and intensifies the monsoon system (Nicholson, 1996). During the early Holocene (11.7–8.2 kya; following Holocene formal stratigraphic designations of Walker et al. (2012)), precessionally-driven high Northern Hemisphere insolation resulted in mesic conditions known as the African Humid Period (AHP), which persisted until falling insolation weakened the monsoons around 5 kya (Kutzbach, 1981; deMenocal et al., 2000; Costa et al., 2014).

The global climate changes and local ecological shifts of the early and middle Holocene constitute the setting for diverse transitions from hunting/gathering to food production in different parts

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of the world – the most significant economic shifts and cultural adaptations in human prehistory, which continue to shape livelihoods and geopolitical relations in today's world. Although farming was the first form of food production on many continents, herding (i.e., keeping domestic animals without sole reliance on livestock for subsistence) preceded plant cultivation in many parts of Africa (Marshall and Hildebrand, 2002). African herding systems relied upon cattle (*Bos taurus*), sheep (*Ovis aries*), goat (*Capra hircus*), and/or donkey (*Equus asinus*), with relative proportions of these animals at archaeological sites varying widely across time and space. Because herding economies are typically associated with some degree of mobility (Smith, 2005), the mechanisms for herding's spread and the nature of social change in early herding economies may have differed profoundly from those found among early sedentary farmers (Hildebrand et al., 2018; Sawchuk et al., 2018).

After livestock appeared in Africa's archaeological record by ~8 kya in the eastern Sahara (Linseele et al., 2016), the spread of herding almost certainly involved a mix of human population movements and adoption of livestock by local hunter-gatherers; these processes may have varied by area. From the Sahara, pastoralism spread south through the Sahel and east into the Horn of Africa (Marshall and Hildebrand, 2002; Lesur et al., 2014). In eastern Africa, herding began around Lake Turkana ~4.7 kya (Barthelme, 1985), shortly after AHP ended in the region; farther south, livestock appeared sporadically at archaeological sites in Kenya's Central Rift and around Lake Victoria beginning ~4 kya, but only became common ~3 kya (Ambrose, 1998; Gifford-Gonzalez, 2000; Prendergast, 2010). At this time, specialized pastoralism began to flourish across central-southern Kenya and in north-central Tanzania (Grillo et al., 2018), with multiple distinctive Pastoral Neolithic (PN) traditions identified in this region between ~3–1.2 kya (Lane, 2004; Lane, 2013).

Eastern Africa presented a new and sometimes challenging context for pastoralism. The Eastern African Rift System's latitude, steep topography, and variable soils derived from volcanic and sedimentary rock sources create complex patterns of rainfall and vegetation that differ from typical Sahelian conditions today (White, 1983), and would have done so in the past (Marshall and Hildebrand, 2002). These factors, together with zoonotic diseases carried by eastern African wildlife, may have led to patchy or delayed establishment of herding in some areas (Gifford-Gonzalez, 2000, 2017). Although social responses such as livestock exchange and mobility are regarded as key factors enabling the spread of herding (Marshall et al., 2011), our understanding of the environmental contexts that created these challenges – and required such responses – has been based more on speculation than on quantitative data.

Many authors have suggested that changing climatic conditions directly or indirectly abetted the spread of herding, positing that as insolation-induced mesic conditions of the AHP gave way to more arid climate regimes after 5 kya (deMenocal et al., 2000; Tierney et al., 2011a; Walker et al., 2012), herders may have followed the monsoon belt as it retreated south. Shifting climate and increasingly erratic rainfall and/or changes in rainfall seasonality, especially after 3 kya, may have prompted the development of social networks and patterns of mobility that enabled herders to thrive, and/or facilitated the adoption of food production by foragers (Marshall, 1990; Smith, 1992; Marshall et al., 2011).

Although the general chronological association between the end of the AHP and the southward spread of herding is clear, defining relations among changes in climate, terrestrial ecology, and human behavior is a complex task. Most archaeological theories about the connections between changes in climate and herder behavior focus on human responses to shifting rainfall and resource availability at a local level, considering such ecological issues as available drinking water and graze; these theories often assume a direct relationship between large-scale climate changes and smaller-scale ecological shifts. But in the absence of local paleoenvironmental proxies, like those presented in this paper, this is a risky assumption. First, the 'start' and 'end' dates for the AHP may vary from area to area (Costa et al., 2014), such that shifts in terrestrial ecology are likely not synchronous among basins (Tierney et al., 2011b; Blome et al., 2012). Second, the relationship between woody cover and rainfall is not linear: though mean annual precipitation and seasonal distribution of rainfall affect percent woody cover, so do herbivore community structure, fire, and soil properties (Bell, 1982; Murphy and Lugo, 1986; Scholes and Archer, 1997; Bradshaw et al., 2003; Good and Caylor, 2011). Third, few empirical records document terrestrial paleoecology and woody cover directly associated with archaeological material. Finally, understanding the social, political, and economic motivations underpinning pastoralists' decisions to move into new areas, or foragers' decisions to adopt livestock (either to cope with increasingly unreliable wild resources, or for political and/or social reasons), will require robust chronologies that couple rich archaeological datasets with high-resolution paleoecological data.

Here we address the first three issues above by developing a multi-proxy paleoenvironmental record for the Lake Turkana Basin (LTB) and the Lake Victoria Basin (LVB) (Fig. 1), during and after the AHP (Table 1), using leaf wax biomarkers and tooth enamel stable isotopes. Our environmental reconstruction indicates that ecology within these two basins responded very differently to changes in climate driven by solar insolation. This multi-proxy approach provides a more nuanced understanding of the relationships among climate, vegetation change, and human behavior in eastern Africa, demonstrating variable ecological responses to climate forcing, and similarly diverse human responses to ecological shifts or stasis. Our results suggest that factors other than ecological change prompted the spread of herding during this time period.

2. Regional setting

2.1. Lake Turkana area

Archaeological and paleoenvironmental fieldwork yielded samples from sites on both sides of Lake Turkana (Fig. 1). Contexts dated to the AHP, when fishing-hunting-gathering is thought to have prevailed, include the excavated archaeological sites of GaJj11 and FxJj12 on the eastern paleoshore, and Lothagam Lokam (GeJi11) on the western paleoshore.[1] Detailed site descriptions, including stratigraphy, dating, faunal remains, and material cultural analysis have been published for GaJj11 (Barthelme, 1985) and Lothagam Lokam (Robbins, 1974). Both contain barbed bone points ('harpoons') and abundant fish refuse, indicating an aquatic-oriented economy. Radiocarbon dates from these sites were obtained from *in-situ* materials removed during excavation, in addition to surface scatter material where relevant (Table 1).

In addition, faunal samples from the surfaces of three sites found during 2012 survey ("Equid Site", "Site AW", "Site 514"[2]) were directly dated using tooth enamel (Table 1), yielding ages that placed them within the AHP. Of these, only Site 514 had diagnostic cultural material on the surface: barbed bone points, faunal material, pottery, ostrich eggshell pieces, and human remains. Post-

[1] The Lothagam Harpoon site (Robbins, 1974) was recently renamed Lothagam Lokam in consultation with L. Robbins and local Turkana, and assigned the SASES code GeJi11 (Goldstein et al., 2017). Site codes follow the "Standard African Site Enumeration System" (SASES) (Nelson, 1971).

[2] None of these sites have been assigned a SASES code.

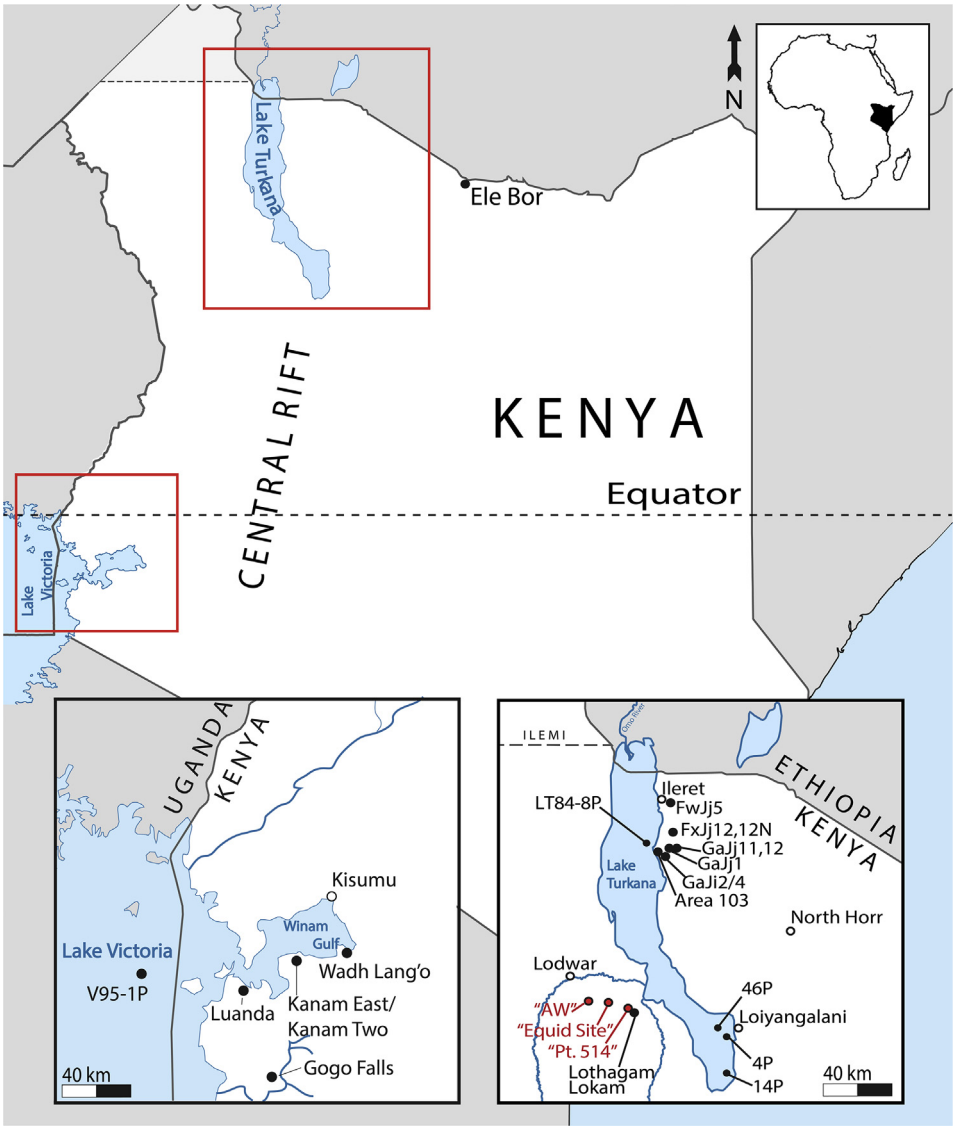

Fig. 1. Map of the study areas. Open circles are cities. Callouts to specific sampling areas in boxes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

AHP samples were sought from the archaeological sites of Dongodien (GaJi4) and adjacent GaJi2, dated via charcoal to ~4.7–4.4 kya (Table 1). Detailed publications of these pastoral occupations (Marshall et al., 1984; Barthelme, 1985) describe abundant mammalian remains, including domestic cattle and caprines, and a novel tradition of intricately decorated pottery (Nderit Ware). In this paper, these adjacent and nearly contemporaneous sites are treated as a single site and referred to as GaJi2/4.

2.2. Inland northern Kenya

The rockshelter site of Ele Bor Site A (EBA) is located ~200 km east of Lake Turkana. At EBA, there is no strong evidence that herders occupied the site (Phillipson, 1984; Gifford-Gonzalez, 2003). Subsistence was based on foraging and hunting, as evidenced by abundant wild vertebrate bones (Gifford-Gonzalez, 2003). All radiocarbon dates were obtained from excavated charcoal and bone at EBA, and indicate early (Horizon C, ~7.5 kya), middle (Horizon B, ~4.6 kya), and later (Horizon A, ~1.1 kya) Holocene occupations (Table 1).

2.3. Lake Victoria area

Three early-middle Holocene sites with evidence for fishing-hunting-gathering (FHG) economies are included in the LVB sample (Fig. 1). The shell middens of Kanam East/Kanam Two (treated here as a single site) and Luanda have evidence for Kansyore pottery and FHG subsistence (Robertshaw et al., 1983). The Kansyore tradition is associated with FHG at shell middens and open-air sites around the basin during much of the Holocene (Dale and Ashley, 2010). Since Kanam was previously undated, here we obtained a new direct date on tooth enamel (Table 1), which correlates well with previously-obtained dates on shell and bone apatite from Luanda (Robertshaw et al., 1983), and which place both sites within the AHP. The third site, Wadh Lang'o, preserves a post-AHP occupation with Kansyore ceramics and evidence of a FHG economy,

Table 1
List of sites sampled, with corresponding radiocarbon dates. Dates generated before 2013 were recalibrated using a mixed calibration curve that incorporates both IntCal13 or SHCal13 in OxCal 4.2; this is essential for sites near the equator, which experience atmospheric influence from both hemispheres. If the components of atmospheric mixing from each hemisphere is unknown, the "Mix_Curve" command with the term "U(0,100)" allows the model to exercise the ability to incorporate any mixture of the two calibration curves, followed by Bayesian model to further constrain dates generated (Hogg et al., 2013; Marsh et al., 2018; Ramsey and Lee, 2016; Reimer et al., 2013; Tryon et al., 2018).

Area and Site	uncal YBP	calBP	sd	Material	Sample ID	Source
Lake Turkana						
"514″	6390 ± 20	7301	39	tooth enamel	AA107305	this study
"AW″	7030 ± 20	7858	45	tooth enamel	AA107306	this study
"Equid Site"	8700 ± 20	9613	39	tooth enamel	AA107310	this study
"Equid Site"	8850 ± 20	9907	116	tooth enamel	AA107311	this study
"Equid Site"	8920 ± 20	10037	77	tooth enamel	AA107307	this study
"Equid Site"	9350 ± 20	10539	39	tooth enamel	AA107308	this study
FxJj12	8355 ± 235	9286	307	bone apatite	Gx-5480-A	Owen at al (1982)
FxJj12	8395 ± 270	9348	359	bone apatite	Gx-5481-A	Owen at al (1982)
Dongodien, GaJi4	4180 ± 53	4692	86	charcoal	Beta-252055	Ashley et al. (2011)
Dongodien, GaJi4	4180 ± 40	4698	78	charcoal	Beta-252053	Ashley et al. (2011)
Dongodien, GaJi4	4240 ± 40	4749	72	charcoal	Beta-252054	Ashley et al. (2011)
GaJj11	8920 ± 130	9963	185	shell	Hel-1276	Owen at al (1982)
GaJj11	9110 ± 130	10244	196	*Etheria*	Hel-1277	Owen at al (1982)
GaJi2	3970 ± 60	4391	100	charcoal	P-2609	Owen at al (1982)
GaJi2	4160 ± 110	4657	145	charcoal	SUA-634	Owen at al (1982)
Lothagam Lokam, GeJi11	6010 ± 160	6851	199	shell	N-1101	Robbins (1974)
Lothagam Lokam, GeJi11	7960 ± 140	8808	185	shell	N-813	Robbins (1974)
Lothagam Lokam, GeJi11	7560 ± 20	8366	24	tooth enamel	AA107312	this study
Lothagam Lokam, GeJi11	8230 ± 180	9139	233	organic seds	N-1102	Robbins (1974)
Ele Bor Site A						
Horizon A	1320 ± 50 AD	599	37	charcoal	P-2612	Phillipson (1984)
Horizon A	480 ± 50 AD	1351	46	charcoal	P-2613	Phillipson (1984)
Horizon A	250 ± 50 AD	1591	68	charcoal	P-2614	Phillipson (1984)
Horizon B	1545 ± 130 BC	3758	168	bone apatite	Gx-5743-A	Phillipson (1984)
Horizon B	1870 ± 170 BC	4199	240	bone apatite	Gx-5744-A	Phillipson (1984)
Horizon B	3200 ± 170 BC	5899	191	bone apatite	Gx-5745-A	Phillipson (1984)
Horizon C	4645 ± 170 BC	7460	157	bone apatite	GX-5158-A	Phillipson (1984)
Horizon D	4895 ± 240 BC	7702	267	bone apatite	GX-5156-G	Phillipson (1984)
Horizon D	5935 ± 220 BC	8761	267	bone apatite	GX-5156-A	Phillipson (1984)
Lake Victoria						
Kanam East, Kanam Two	7400 ± 20	8208	56	tooth enamel	AA107309	this study
Luanda	6740 ± 80	7581	67	shell	Pta-3139	Robertshaw et al. (1983)
Luanda	8240 ± 245	9144	307	bone apatite	GX-8743	Robertshaw et al. (1983)
Wadh Lang'o (110–113 cm bed)	1420 ± 30	1308	23	charcoal	OS-57500	Prendergast (2010)
Wadh Lang'o (170–180 cm)	1950 ± 35	1876	46	charcoal	OS-59768	Prendergast (2010)
Wadh Lang'o (250–260)	3740 ± 35	4061	62	charcoal	OS-59681	Prendergast (2010)
Wadh Lang'o (290–300 cm)	3770 ± 35	4104	68	charcoal	OS-61970	Prendergast (2010)
Wadh Lang'o (300–310 cm)	3850 ± 30	4234	71	charcoal	OS-59682	Prendergast (2010)
Gogo Falls	1900 ± 70	1814	86	charcoal	HAR-6260	Robertshaw (1991)
Gogo Falls	1710 ± 70	1601	89	charcoal	HAR-6261	Robertshaw (1991)

with occasional remains of livestock suggesting forager-herder contact (Lane et al., 2007; Prendergast, 2010).[3] This occupation is dated to ~4.2–4 kya, based upon associated charcoal (Table 1).

The later Holocene occupations of Wadh Lang'o, together with the site of Gogo Falls, are considered the only definitive herding contexts in the LVB dataset. At Wadh Lang'o, post-Kansyore occupations document distinctive material culture traditions and economic shifts. Elmenteitan pottery, a PN tradition, appears ~1.9–1.3 kya based on associated charcoal, coinciding with shifts in lithic production and increased cattle and caprine remains, and with continuity in wild and aquatic faunal exploitation (Prendergast, 2008). The uppermost levels of Wadh Lang'o, associated with Iron Age Urewe ceramics, are not included in the present sample.

At Gogo Falls, the archaeological sequence parallels that of Wadh Lang'o, with Kansyore, Elmenteitan, and Urewe material traditions, and with mixed FHG and herding subsistence economies; several radiometric determinations on obsidian, bone, and charcoal are available and sometimes conflict with one another (Robertshaw, 1991; Karega-Munene, 2002). While Wadh Lang'o dates consistently follow the stratigraphic sequence, this is not the case at Gogo Falls, where post-depositional mixing is a concern. The present sample includes only faunal remains from the relatively well-dated Elmenteitan contexts, ~1.8–1.6 kya based upon associated charcoal (see Table 1). At both sites, a lack of direct dates makes for poor chronological resolution for the initial appearances of livestock, but most indicators suggest a patchy introduction of and gradual increase in livestock amid long-term continuity in FHG subsistence strategies (see discussion in Prendergast, 2008, 2010).

3. Materials and methods

This study compares and integrates data sources that record events at different geographical and temporal scales. Global climate perspectives are drawn from published records; basinal climate

[3] There have been multiple excavations at Wadh Lang'o and Gogo Falls. Samples in this study come from the 2001 excavations at Wadh Lang'o (Odede, 2002; Prendergast, 2008, 2010), and from the 1983 excavations at Gogo Falls (Robertshaw, 1991).

records (precipitation) are established through δD in leaf wax biomarkers from LTB (this study; Morrissey, 2014) and LVB (Berke et al., 2012a). Basin-scale ecological responses to these climate events are assessed via $\delta^{13}C$ values in leaf wax biomarkers, showing vegetation change or continuity within the watersheds of LTB (this study; Morrissey, 2014) and LVB (Berke et al., 2012b). Local ecological reconstructions rely on $\delta^{13}C$ and $\delta^{18}O$ signatures of tooth enamel from herbivores recovered at archaeological sites near the Lake Turkana paleoshore, inland areas in northern Kenya, and the Lake Victoria paleoshore and its tributaries (this study).

Some sources of new data presented in this article can pose interpretive challenges. Leaf wax biomarkers provide multiple levels of environmental information: leaf wax δD serves as a proxy for changes in rainfall (Schefuβ et al., 2005; Niedermeyer et al., 2010; Polissar and Freeman, 2010; Kahmen et al., 2013; Magill et al., 2013b), and leaf wax $\delta^{13}C$ can reveal changes in representation of C_4 plants (Eglinton and Hamilton, 1967; Freeman and Colarusso, 2001; Sinninghe Damsté et al., 2011). However, leaf wax biomarkers may have been transported into lake basins by major river catchments, such as the Omo River for LTB (Cerling, 1986). Also, rates of leaf wax production may vary by taxon and according to seasonal and longer-term environmental fluctuations, such that carbon isotope values do not always serve as a direct measure of landscape heterogeneity (Diefendorf et al., 2011; Hoffmann et al., 2013; Carr et al., 2014). However, diachronic changes in leaf wax stable isotope values can serve as reliable indicators of climatic (δD) and environmental ($\delta^{13}C$) changes within the catchment area over time.

Isotopic values of herbivore teeth also can raise interpretive questions. When making comparisons between modern fauna and archaeofauna, it is important to consider whether sampled archaeofauna represent the natural fauna that existed at the time. Variable human hunting practices and prey selection may have imposed biases, and other (social) factors or constraints may have influenced faunal transport, processing, and discard (Hawkes et al., 1997; Kennett and Winterhalder, 2006), while taphonomy may have affected preservation of sites and remains. Although no single site's faunal assemblage is a perfect sample of its surrounding environment, the high degree of variation among assemblages suggests that behavioral and taphonomic biases are not uniform. Rather, intra- and inter-assemblage variation constitutes important evidence for the range of fauna (and environments) to which prehistoric people may have had access.

Even considering these issues, the proxies examined here represent the some of the best available windows into the past. Furthermore, the proxies used in this study do reflect the environments in which humans lived and with which they interacted, because they come from the archaeological sites and the basins occupied by ancient people (see discussion in Levin, 2015). To minimize bias in our paleoenvironmental reconstruction, we sampled all available herbivore teeth excavated or surface collected from a particular site, and only reduced sample sizes of certain taxa in cases where they were overrepresented (>30 individuals).

3.1. Sedimentary leaf wax biomarker analysis

Early Holocene lacustrine sediments were collected from Area 103 near Lake Turkana (Fig. 1). Stratigraphic correlation to previous maps of these deposits (Owen and Renaut, 1986) provides ages for the sediments (11.5–5.8 kya, dates from mollusk shells *in situ*). Compound specific isotope analysis (CSIA) was completed at the Pennsylvania State University. Eighteen leaf wax biomarker samples were extracted using an Automated Solvent Extractor in 9:1 DCM:Methanol, purified by column chromatography. The resultant polar fraction containing *n*-alkanoic acids were derivatized into fatty acid methyl esters (FAMEs) for isotope analysis using a phthalic acid standard (Arndt Schimmelmann, Indiana U.) with a known $\delta^{13}C$ value of −73.16‰. $\delta^{13}C$ values of FAMEs were corrected to their original carbon isotopic value after methylation using a mass-balance correction of the derivatization standard. Percent C_4 input was calculated using endmember values from previously published values (−22 to −34‰) (Castañeda et al., 2009; Magill et al., 2013a).

3.1.1. Tooth enamel selection and isotopic analysis

Tooth enamel samples (n = 368) taken via identical sampling strategies from similar taxa found at Holocene archaeological sites in LTB and LVB, and at the site of EBA, were analyzed for $\delta^{13}C$ and $\delta^{18}O$. Teeth were sampled from collections in National Museums of Kenya (NMK), and from collections made during 2011 and 2012 surveys in the Turkana Basin. In the interest of scope, we did not analyze $\delta^{18}O$ data in this manuscript, though it is presented with the raw data in Appendix Table A.2. The resulting dataset substantially exceeds previous Holocene isotope studies in eastern Africa in sample size and in geographic and temporal scope (Ambrose and DeNiro, 1989; Ambrose and Sikes, 1991; Balasse and Ambrose, 2005).

Samples were photographed, drilled with a diamond tipped drill bit using a Dremel hand-held drill, and stored in 1.7 ml centrifuge tubes, following destructive sampling procedures outlined by the NMK. Samples were analyzed using established procedures: digestion with H_3PO_4 for tooth enamel following pre-treatment with 0.1 M buffered acetic acid. The resulting CO_2 gas was analyzed on a dual-inlet isotope ratio mass spectrometer. Standard deviation of internal standards (Carrara marble, MHS, FRS) was between ± 0.1–0.2‰. Modern samples were corrected to MHS and fossil samples to FRS for the temperature effect for phosphoric acid digestion of tooth enamel (Passey et al., 2007). Isotope data are reported in the standard per mil (‰) notation:

$$\delta^{13}C = (R_{sample}/R_{standard}\text{-}1)^{*}1000$$

When comparing isotope values of modern and ancient tooth enamel, one must correct for changes in the carbon isotopic composition of the atmosphere due to recent combustion of fossil fuels (Francey et al., 1999). This changing isotopic composition of the atmosphere affects the $\delta^{13}C$ values of herbivore food sources, and thus tooth enamel isotopic composition (Cerling and Harris, 1999). A correction of +1.6‰ was applied to modern comparative isotope date to generate endmember values for interpreting dietary composition of ancient fauna. Data are presented as $\delta^{13}C_{1750}$ to denote that this correction has been applied.

3.1.2. Assessment of herbivore diets

Dietary designations for herbivores are based on estimated consumption of C_4 plants (tropical grasses) and C_3 plants (trees, shrubs, herbs), which is calculated using a hypothetical 100% C_4 diet and an isotope enrichment (ε^*) between diet and ruminant tooth enamel of 14.1‰, which we apply to all herbivores in the dataset, as ε^* is similar in non-ruminants (Cerling and Harris, 1999, and discussions therein). Estimated carbon isotope composition of tooth enamel for a 100% C_4 diet is based on the average isotopic value of modern C_4 plants in eastern and central Africa (−12.9‰, n = 764), which are based on mixing lines of mesic and xeric adapted plants, and for which uncertainty in ε^* across a variety of taxa is accounted (Cerling, 2013; see discussions in Cerling et al., 2015). These values were then plotted in ternary diagrams in R, following Cerling et al. (2015).

Ternary plots (Fig. 2) were assembled from assigned feeding behavior classifications of herbivores from the site using herbivore

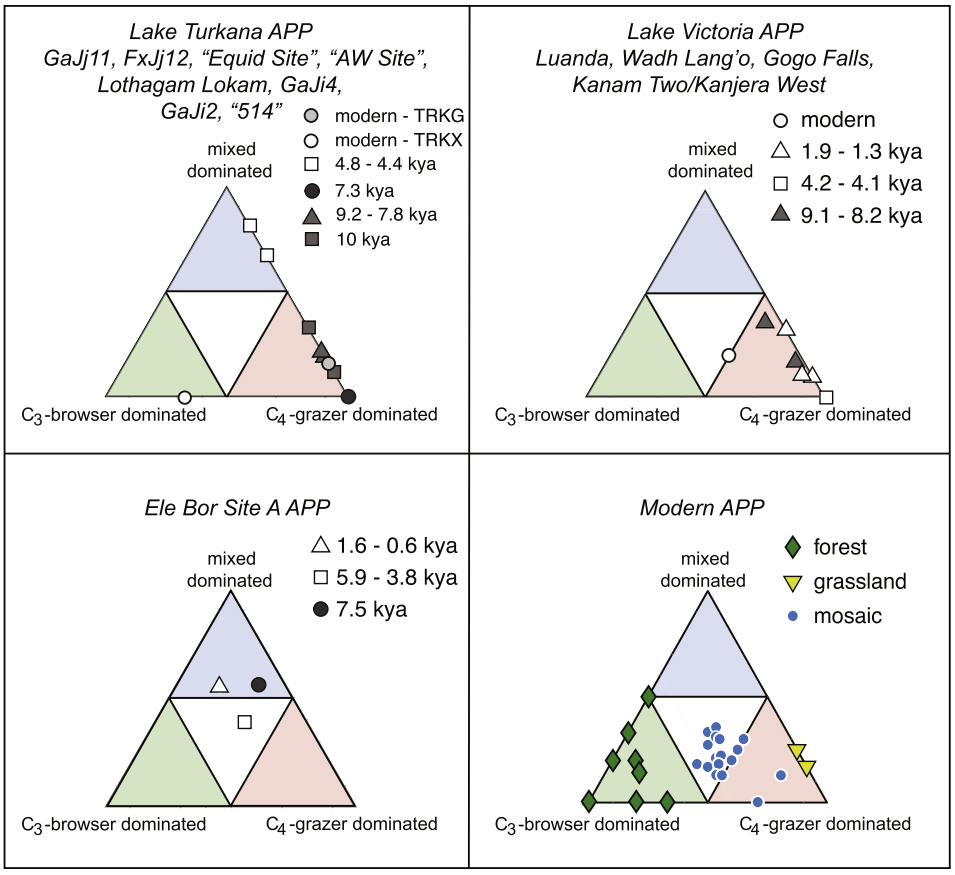

Fig. 2. Ternary plots of dietary designations from archaeological and modern herbivore tooth enamel isotopes, showing changes in percent feeder type over time. Modern APP (Artiodactyla-Perissodactyla-Proboscidea) plot from (Cerling et al., 2015). Isotope ranges for each feeder type are given in SI section 3.

tooth enamel values. Each apex of the ternary plot represents 100% composition of a three-component object—in this case, herbivore diet. Points are plotted within the ternary plot according to their composition. All herbivore tooth enamel values were divided into G:M:B composition as percentages of the entire faunal assemblage sampled at a specific site, following the methods of Cerling et al. (2015). Grazers (G) are defined as herbivores with dietary isotope values greater than −1‰, mixed feeders (M) are defined as having dietary values between −1‰ and −8‰, and browsers (B) are defined as having dietary values less than −8‰.

Ages for specific archaeological sites or stratigraphic units within sites were assigned based on average age of the site or stratum from all available dates presented in Table 1. Archaeological sites or stratigraphic units were then grouped into chronological intervals to facilitate comparison across time and space. G:M:B ratios for each site (or certain strata within a site) were plotted on ternary diagrams in R using packages ggplot2 (Wickham, 2016) and ggtern (Hamilton, 2017). Ternary plots of modern Kenyan environments were reproduced from data presented by Cerling et al. (2015). Chronological intervals based on standard deviation of corrected dates and composed of the sites (and/or strategraohic units within sites) that are presented in Table 2.

Isotope data from archaeological specimens are compared to previously published modern values (Kohn et al., 1996, 1998; Schoeninger et al., 2002; Cerling et al., 2008; Blumenthal et al., 2017), and to leaf wax biomarkers for LTB (this study, Morrisey, 2014) and LVB (Berke et al., 2012b) in order to assess how site-specific ecology (indicated by faunal tooth enamel isotopes) relates to basinal scale vegetation patterns (via leaf wax $\delta^{13}C$), which may or may not parallel climatically-triggered changes in rainfall (via leaf wax δD and paleo lake terraces).

4. Results

LTB climate proxies show that insolation forcing exerted a strong effect on moisture delivery and lake levels (Fig. 3A and B). As the AHP ended locally ~5kya, a rapid drop in Turkana lake levels is demonstrated by radiocarbon dated paleo-beach terraces (Garcin et al., 2012) and changes in strontium isotopes (van der Lubbe et al., 2017). This was exacerbated by cessation of overflow from the Chew Bahir Basin, which occurred around the same time (van der Lubbe et al., 2017). An increase in leaf wax δD values (Fig. 3C; Morrissey, 2014) show that LTB precipitation changes correlated with globally recorded insolation effects, such as increases in dust input to the eastern Atlantic (deMenocal et al., 2000; Tierney and deMenocal, 2013).

Vegetation changes in LTB are traced through stable carbon isotope values of leaf wax biomarkers (Fig. 3D,F) from lacustrine sediments and piston cores (Morrissey and Scholz, 2014) by calculating $\%C_4$ input to lake sediments using previously published C_3–C_4 endmember values of African flora (Castañeda et al., 2009; Magill et al., 2013a). The Lake Turkana catchment includes the Ethiopian highlands via the Omo River, and western Kenya highlands via the Turkwel and Kerio Rivers. Piston core data from the southern end of the lake (Fig. 3D), where sediments brought via the Kerio and Turkwel accumulated slowly (Morrissey, 2014; Morrissey and Scholz, 2014), show low C_4 plant biomass (20% or less) from 12 kya until ~4 kya, just after herding takes hold, followed by an

Table 2
Summary of sample locations and chronology.

Area & time interval	Sites and dates (midpoint of age range probability distributions)
Lake Turkana Basin	
10 kya	Equid Site (10.0 kya); GaJi11 (10.1 kya)
9.2–7.8 kya	Lothagam Lokam/GeJi11 (8.3 kya), Site AW (7.9 kya)
7.3 kya	Site 514 (7.3 kya)
4.8–4.4 kya	GaJi2 (4.5 kya); GaJi4/Dongodien (4.7 kya)
0 kya (modern)	TRKX* [Inland Turkana] and TRKG* [Shoreline Turkana]
Ele Bor Site A	
7.5 kya	EBA Horizon C (7.5 kya)
5.9–3.8 kya	EBA Horizon B (4.6 kya)
1.6–0.6 kya	EBA Horizon A (1.3 kya)
Lake Victoria Basin	
9.1–8.2 kya	Luanda (8.4 kya), Kanam East/Kanam 2 (8.2 kya)
4.2–4.1 kya	Wadh Lang'o: 310-300 cm (4.2 kya), 300-290 cm (4.1 kya), 260-250 cm (4.1 kya)
1.9–1.3 kya	Wadh Lang'o: 180-170 cm (1.9 kya), 113-110 cm (1.3 kya), Gogo Falls (1.7 kya)
0 kya (modern)	RFTV* [Kenya Rift Valley]

* see Cerling et al., (2015).

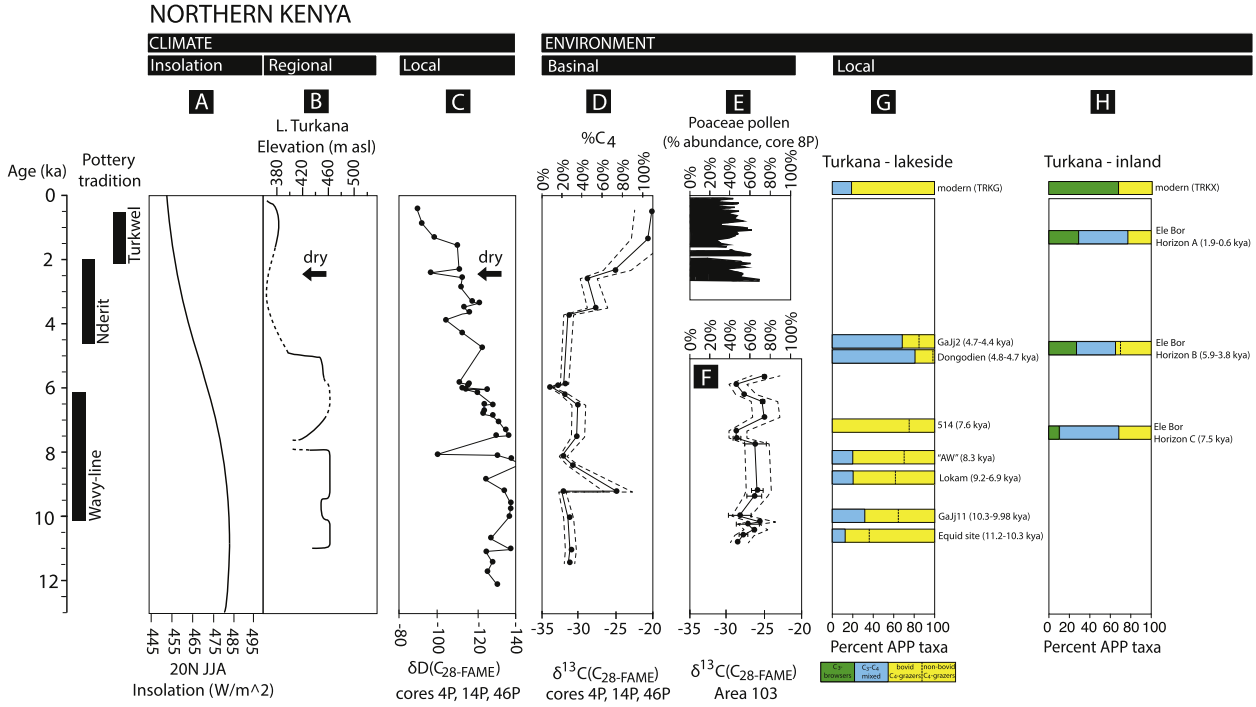

Fig. 3. A – Solar summer insolation (June-July-August, "JJA") at 20 N; B - Lake Turkana paleolake terraces (Garcin et al., 2012); C – leaf wax δD values from sedimentary n-alkanoic acids from piston cores (Morrissey, 2014); D – leaf wax $\delta^{13}C$ values from sedimentary n-alkanoic acids piston cores (Morrissey, 2014); E – Poaceae (grass) pollen from core 8P (north basin)(Mohammed et al., 1995); F - $\delta^{13}C_{wax}$ values from sedimentary n-alkanoic acids from terrestrial lacustrine sediments (this study); G – dietary designations from tooth enamel isotopes of archaeological sites in the Lake Turkana Basin (this study; modern data from Cerling et al., 2015); H – dietary designations from tooth enamel isotopes from the archaeological site of Ele Bor, Site A (this study).

increase in C_4 biomass to ~100%. In contrast, northern area samples – from Area 103 (Fig. 3F) and LT84–8P (Fig. 3E) – may reflect faster deposition of sediments by the Omo River from the Ethiopian highlands and northern areas of the basin (Cerling, 1986). Data from Area 103 (Fig. 3F) show several fluctuations between 35 and 75% from 10.5 to 6 kya, but no clear direction of change. Pollen data from Core LT84–8P, which covers the period 2.5 kya to present (Fig. 3E) show Poaceae (grasses, which comprise the vast majority of C_4 plants) fluctuating but generally high (>40%) (Mohammed et al., 1995). Divergent results from these two sampling areas suggest that northern vs. southern parts of the LTB differed in their ecological responses to climatic events.

The LVB Holocene sequence has an almost uninterrupted record of leaf wax δD, leaf wax $\delta^{13}C$, and pollen values from piston cores (Fig. 4), offering the opportunity to compare these commonly used but rarely integrated proxies (Feakins et al., 2005; Levin, 2015). Assessing climate effects, leaf wax δD values show gradual aridification of the LVB (Fig. 4B). Its moisture decline is less dramatic than that seen via the leaf wax δD sequence from Lake Challa, 450 km to the SE (Tierney et al., 2011b), but is in step with both eastern Atlantic marine sediments leaf wax δD records (Niedermeyer et al., 2010) and insolation forcing (Berke et al., 2012a) (Fig. 4A).

Some proxies suggest climatic changes may have triggered ecological responses in the LVB. Moraceae (moist-adapted trees such as *Ficus*) decrease gradually from 8 kya to the present (Fig. 4D). Poaceae pollen remain <10% from 10 kya to ~4.5 ka, after which

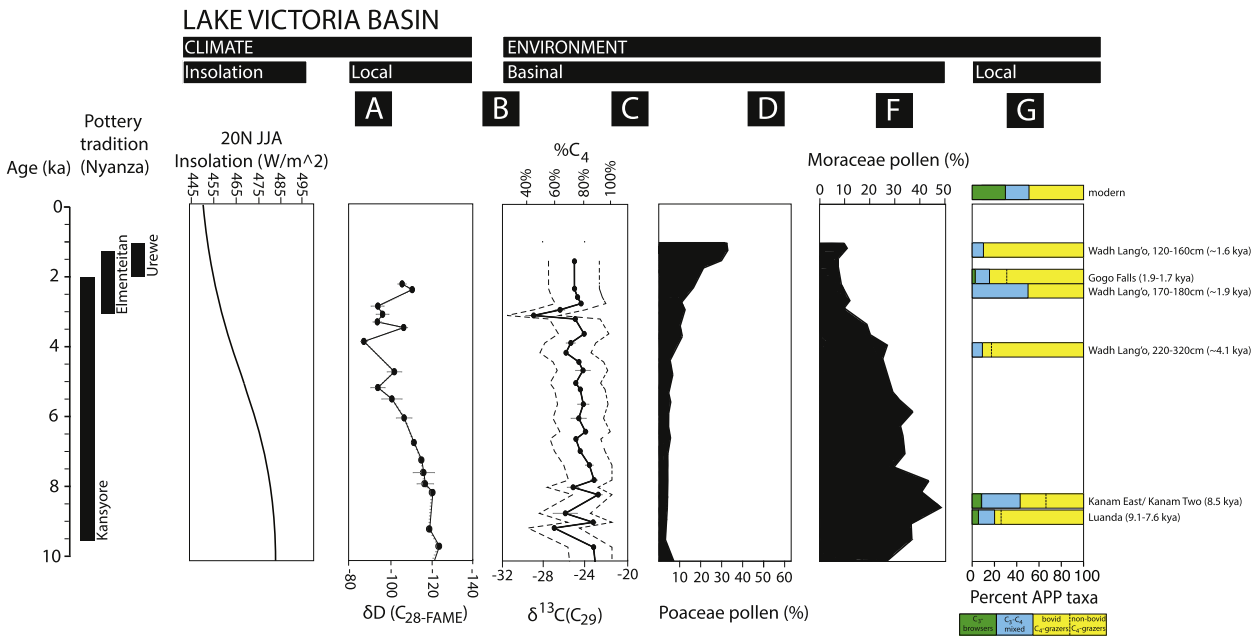

Fig. 4. A – Solar summer insolation (June-July-August, "JJA") at 20 N; B – leaf wax δD values from sedimentary n-alkanes in piston cores from Lake Victoria (Berke et al., 2012a); C – leaf wax $\delta^{13}C$ values from sedimentary n-alkanes in piston cores from Lake Victoria (Berke et al., 2012a); D – Poaceae (grass) pollen from Pilkington Bay piston cores (Kendall, 1969); E – Moraceae (moist trees) pollen from Pilkington Bay (Kendall, 1969); F – dietary designations from tooth enamel isotopes from modern (Cerling et al., 2015) and archaeological sites in the Lake Victoria Basin (this study).

they gradually rise to 30% by ~1.5 kya (Fig. 4F). An inverse relation between these two pollen types is to be expected, and these changes are consistent with the LVB leaf wax declines in δD. Curiously, despite these multiple indications of aridity, LVB leaf wax $\delta^{13}C$ values indicate consistently substantial C_4 input to the sedimentary record (Fig. 4C). Although values fluctuate (40–80%), LVB leaf wax biomarkers provide no evidence for gradual directional change in C_4 plant representation.

Stable isotope data from archaeological herbivore tooth enamel that allow comparisons between the two basins are presented in the SI (Appendix Tables A.1-A.3). An in-depth discussion of sampling bias and caveats inherent to interpreting archaeological stable isotope values is also given in the SI. Percent GMB (grazers, mixed feeders and browsers) for each archaeological site was calculated from these $\delta^{13}C$ values following the guidelines of Cerling et al. (2015; methods in the SI). Ternary diagrams (Fig. 2) of major Artiodactyla-Perissodactyla-Proboscidea (APP) faunal dietary designations through time reveal dietary trends among herbivores in each community and show that herbivores' diets in the two basins responded differently to Holocene monsoon changes.

Modern faunal diets from the inland Turkana region (TRKX, dwarf shrubland; Cerling et al., 2015) can be characterized as predominately C_3-based (67%), whereas those from lakeside ecosystems (TRKG, grassland) are predominately C_4-based (83%). In the past, APP fauna in the LTB consumed predominantly C_4 resources 10.5–7 kya; by 5 kya, mixed C_3–C_4 diets had become more typical. At EBA ~200 km inland, APP faunal diets were dominated by mixed C_3–C_4 resources from 7.0 to 0.6 kya, resembling the feeding behavior of TRKX fauna today. By contrast, APP faunal diets from LVB have been C_4-dominated throughout the Holocene. Dietary designations of the LTB and LVB archaeofauna are placed into contexts of climatic and ecological changes that occurred in each basin (Figs. 3 and 4). These data, supplemented by other available paleoecological data for each basin, indicate contrasting ecological responses to climate forcing.

5. Discussion

Intra- and inter-basinal comparisons reveal important local differences in ecological response to climate change. We first compare proxy records in and around LTB, and then do so for LVB. A clear understanding of the nuances of each basin's record allows us to examine contrasts between them, and to examine archaeological records for foraging and early food production in light of our results.

5.1. Proxy comparisons within the Turkana Basin and inland areas

In LTB, the $\delta^{13}C$ values of archaeofauna ~10–7 kya (at GaJi11, Lothagam Lokam, Equid Site, and Site AW) indicate mostly C_4 diets, though mixed C_3–C_4 diets occur in low abundance (Fig. 3G, Appendix Table A.1). These results parallel isotopic signatures from the modern lakeside ecosystem (TRKG, Fig. 3G). However, by ~4.7 kya at GaJi2/4, faunal isotopic signatures had shifted: C_3 plants were more prevalent in the diets of herbivores found at these adjacent and nearly contemporaneous sites (>60% APP taxa, Fig. 3G), which hold eastern Africa's earliest evidence for livestock (Marshall et al., 1984; Barthelme, 1985).

These faunal isotopic results contrast with basinal vegetation proxies. Piston cores from southern Lake Turkana show low C_4 inputs to the Kerio and Turkwel River catchments until 3.5 kya and increasing C_4 after 2.5 kya (Fig. 3D). In northern Lake Turkana, piston cores and pollen records show moderate representation of C_4 plants and Poaceae pollen in the Omo River watershed through most of the Holocene. Thus the ~4 kya increase in C_3 diets among herbivores along the shores of Lake Turkana—as seen at GaJi2/4—did not stem from an increase in C_3 biomass across the entire basin.

Rather, this disjunction may be explained by orographic effects: because highland areas have more precipitation than lowlands overall, the end of the AHP may have affected highland vegetation

(carried into the leaf wax biomarker record) differently than lowland vegetation (reflected in the faunal isotopic record). In highland areas, declining precipitation may have triggered shifts from C_3-dominated montane forests to more mixed grassy woodland combinations richer in C_4 plants; the jump in C_4 representation appears to have been more dramatic in equatorial highlands feeding the Turkwel and Kerio Rivers, than in the Ethiopian highlands feeding the Omo River, given the records from the piston cores. In contrast to both, the lowland areas near Lake Turkana would have captured less rainfall than highland areas throughout the Holocene: during the AHP rainfall they may have sustained grassy vegetation, but as rainfall declined at the end of the AHP, C_4 grasslands near the lake may have given way to more xeric-adapted C_3 bush- and shrublands.

Other explanations are also possible for temporal shifts in herbivore diet around Lake Turkana. Because the GaJi2/4 faunal assemblages have domestic taxa not found in fishing-hunting-gathering (FHG) sites—including Caprini and *Bos taurus* (Appendix Table A.2) – early and middle Holocene datasets are not directly comparable. Additionally, wild taxa not previously seen in our sample are found at GaJi2/4, such as Aepycerotini and Antilopini. Their presence could signal either faunal turnover triggered by local vegetation changes, and/or novel hunting strategies or mobility patterns by people who practiced herding.

Isotopic records for wild animals reveal some unexpected patterns of dietary preferences. Throughout the Holocene LTB sequence, alcelaphines and equids – which are typically regarded as grazers or hyper-grazers in modern contexts – exhibited lower carbon isotope values (more C_3 input) than their modern counterparts (Appendix Table A.2) (Cerling et al., 2015). It thus appears that their diets included more non-grass vegetation than is typical for grazers today. Yet the opposite is true for Antilopini and Neotragini at ~4.7 kya: these medium-sized and dwarf antelopes at GaJi2/4 consumed a higher proportion of C_4 plants (grasses) than their modern counterparts.

Caprines first appear in LTB at GaJi2/4. Sheep and goat cannot be morphologically distinguished in these assemblages, but most or all were likely goats due to lower carbon isotope values (Balasse and Ambrose, 2005; Chritz et al., 2015). Interestingly, these small livestock parallel the small wild antelopes at GaJi2/4 in showing more C_4 intake than their modern counterparts. Changing environmental circumstances – not reflected in the leaf-wax proxies discussed here – may have similarly impacted these small bovids. Alternatively, the higher prevalence of C_3 in the diet of modern caprines could be due to overgrazing today (cf. Prendergast et al., 2018).

The comparative tooth enamel isotope record from EBA, 200 km east of Lake Turkana and 500 m higher in elevation, can reveal inland ecological trends in northern Kenya. The site's four occupational horizons (Horizons A-C, ~7.4–0.6 kya, Table 1) bracket and coincide with the advent of herding in Kenya—but contain almost entirely wild fauna, with bovids (e.g., tragelaphines, Appendix Table A.2) and other herbivores (e.g., giraffe) that are classified as browsers (Gagnon and Chew, 2000; Cerling et al., 2003). Faunal assemblages and isotopic dietary indicators are similar across Horizons A, B and C (D could not be sampled; Fig. 3, Appendix Table A.2), indicating that the environment remained ecologically stable, with C_3 plants dominating during and after the AHP. Archaeofaunal diets from EBA resemble those from TRKX (inland Turkana) modern fauna, indicating a similar scrubland environment from ~7.7 kya to recent times (Fig. 3H). Overall, wild bovids from Ele Bor did not shift their diets over the Holocene, whereas the diets of wild bovids from lakeside archaeological sites did shift.

5.2. Proxy comparisons within the Lake Victoria Basin and inland areas

In LVB, herbivore dietary isotopes across a range of taxa indicate an overall abundance of C_4 plants throughout the Holocene, with fewer mixed C_3–C_4 herbivore diets; only rarely can individuals be considered pure browsers (Figs. 2 and 4G). At the early Holocene FHG sites of Luanda and Kanam East/Kanam Two, herbivores with C_3-dominated diets are present but scarce (<10%), and such browsers are absent or nearly absent in both earlier (Kansyore/FHG) and later (Elmenteitan/PN) contexts at Wadh Lang'o, and in the Elmenteitan/PN contexts at Gogo Falls. As noted earlier, these FHG and PN contexts contain many of the same taxa, since there is strong continuity in exploitation of wild game from Kanyore to PN eras (Appendix Table A.3). While there are no modern faunal isotopic data from LVB for comparison, we note that modern fauna from the Central Rift Valley (RFTV; Cerling et al., 2015), c. 150 km to the east ("modern", Fig. 4G), show interesting contrasts. Most archaeofauna in LVB were consuming C_4 foods, with lower representation of C_3 browsing diets and C_3/C_4 mixed diets; isotopes from modern herbivore tooth enamel indicate that the diets of some taxa (including tragelaphines and *Potamochoerus*) have only recently included more C_3 foods (Appendix Table A.3). Although the modern RFTV dataset is not an ideal comparison, it is currently the nearest possible comparison we have for the ancient fauna in this area.

The strong C_4 component in ancient LVB herbivore diets is notable, given that prior zooarchaeological work identified taxa such as bushbuck, reedbuck, and waterbuck, and interpreted these as indicating semi-closed bushy environments in the past (Robertshaw et al., 1983; Marshall and Stewart, 1995; Prendergast, 2010). Many of these taxa are included in the present isotopic sample (Appendix Table A.3). However, open grasslands-adapted taxa such as alcelaphines, buffalo, warthog, and zebra are also found at LVB sites, and were also sampled in this study. The overall results, from both groups of fauna, indicate access to abundant grasslands, in contrast with prior zooarchaeologically-informed interpretations of environment (see also Chritz et al., 2015).

The LVB herbivore dietary records and leaf wax $\delta^{13}C$ records agree, both showing minimal effects from changing climate and insolation forcing on local ecology (Fig. 4C,G). These two proxies may be similarly spatially integrated, although herbivore home ranges are variable and faunal samples carry their own biases, such as food choices by herbivores, prey selection by humans, and taphonomic biases at archaeological sites (Gannes et al., 1997). Curiously, Lake Victoria's ecological continuity (indicated by faunal isotopes and leaf wax $\delta^{13}C$) contrast with proxies that show a strong insolation effect. Gradual increases in leaf wax δD values (Fig. 4B), and pollen data that show gradual declines in Moraceae (moist-adapted trees) and corresponding increases in Poaceae (grasses), all parallel declines in insolation (Fig. 4A,D,F).

How do we reconcile the LVB's seeming climatic sensitivity, as seen through leaf wax δD and pollen, with its apparent ecological continuity, reflected in leaf wax $\delta^{13}C$ biomarkers and tooth enamel showing long-term prevalence of C_4 grasses and grazing behavior? First, pollen integrates a much larger area within the catchment than leaf waxes, and may therefore reflect a more generalized regional response to decreasing insolation (Bunting et al., 2004; Sugita, 1994). But the discrepancy between change in leaf wax δD vs. continuity in leaf wax $\delta^{13}C$ is more intriguing, because these two proxies derive from the same samples that operate at an identical geographic scale. One must conclude that although decreasing insolation resulted in increasingly arid conditions, as indicated by

higher δD values around Lake Victoria, this was not causing meaningful change in vegetation.

5.3. Implications of inter-basin proxy comparisons

Comparison of multiple proxy records for different lake basins and inland areas in eastern Africa reveals localized ecological responses to global climatic events. Both LTB and LVB record changes in precipitation (via leaf wax δD, Figs. 3C and 4C), demonstrating that decreasing insolation had a direct effect on local climate in both locations. However, vegetation—as seen through leaf wax $\delta^{13}C$ and pollen records—does not show a consistent basin-to-basin response to climate change. In northern LTB tributaries, grasses constituted a substantial portion of the vegetation throughout most of the Holocene (Fig. 3E and F). In southern LTB tributaries, grasses were initially a minor vegetative component but dramatically increased ~3.5kya, achieving near-dominance by 2.5kya (Fig. 3D). Around tributaries for eastern Lake Victoria, leaf wax $\delta^{13}C$ values fluctuated but remained high overall, suggesting C_4 grasses were abundant, comprising 79–90% of vegetation, while regional pollen records suggest a gradual increase in grasses beginning ~4 kya. None of the sampled LVB vegetation proxies shows a sharp change coinciding with the end of the AHP.

Herbivore diets also show localized patterns of change or stasis. Around Lake Turkana, herbivore diets emphasized C_4 plants from ~11–7 kya, dramatically shifting to more mixed C_3/C_4 diets after 5 kya, when herding took hold near the lakeshore. By contrast, long-term dietary continuity is seen inland at EBA, where mixed C_3/C_4 diets dominate for the entire occupation sequence (7.5–0.6 kya). Similarly, herbivore diets in LVB are consistent throughout the Holocene, but in this location they emphasize C_4 plants, despite diverse mammalian taxa including those usually interpreted as bush-adapted species.

Based on these observations, it is difficult to argue that climate change or ecological change acted as “push” or “pull” mechanisms for the spread of herding across the entirety of eastern Africa. Nuanced comparison of multiple proxies shows that climate changes were locally evident, but did not always trigger dramatic vegetation changes. Herbivore diets show shifts in one setting (Turkana shoreline), but stasis in others (EBA, LVB). It is clear that any causal links between global climate change, local ecological shifts, and the advent of herding must be explored at the basinal scale, via careful juxtaposition of paleoenvironmental and archaeological data. Here, we attempt to do just this, while acknowledging the spatial patchiness and poor temporal resolution of parts of the eastern African Holocene archaeological record.

5.4. Environmental and archaeological records from possible source areas

Factors shaping the spread of herding also encompass environmental and cultural conditions in source areas. LTB likely received herding technology and/or populations from South Sudan and/or far southern Ethiopia.

Conflict in South Sudan has impeded paleoenvironmental and archaeological research, and most surveys and excavations have yielded material <2 kya (reviewed by Davies, 2014). At Lokabulo and Jebel Tukyi Rockshelters (respectively 300 and 650 km WNW of the Omo Delta), deep excavation levels yielded pottery with the kinds of comb-stamp, wavy line, and rocker stamp decorations that are typically associated with FGH economies. At Lokabulo, these deep contexts yielded wild fauna, whereas at Jebel Tukyi they held a mix of wild and domestic faunal remains; at both sites, dates for these deep contexts were problematic (David et al., 1981). Rockshelter excavations at Itohom and Lulubo (respectively 280 and 360 km W of the Omo Delta) also yielded ceramic LSA layers with comb-stamped pottery and problematic dates; fauna did not preserve at Lulubo, and excavators at Itohom regarded “the presence of domestic animals in LSA times [as] an open question” (Robertshaw and Mawson, 1981:65). Pottery found during surveys and excavations at open-air sites ~450 km WNW of the Omo Delta hints that a few potentially relevant contexts might exist at the sites of Nyany, Kat (lowest levels), and Jokpel (an isolated find); however these contexts were never dated radiometrically (Robertshaw, 1984; Robertshaw and Siiriäinen, 1985).

In southern Ethiopia's Chew Bahir Basin, elemental analysis indicates periodic droughts during the AHP, which terminated locally between 6 and 5 kya (Foerster et al., 2014). Archaeology in highland southwest Ethiopia (350 km north of the Omo Delta) shows livestock present by 2 kya, but insufficient data to examine the critical period of 5–4 kya (Hildebrand et al., 2010). Some 700 km north of the Omo Delta, at the junction of the Ethiopian Rift and the Afar Depression, near-surface deposits at Lake Besaka yielded three teeth tentatively identified as *Bos*; nearby finds of a stone bowl, pottery, and charcoal dated to 3.8–3.4 kya led Clark and Williams (1978) to propose southern Ethiopia as a potential route for the spread of herding to LTB; Brandt (1982) raises caveats regarding association and context.

Herders entering LVB most likely came from the Central Rift Valley and adjacent plains of Kenya. Here paleoecological proxies are abundant and diverse: isotopic data from soil organic material (Ambrose and Sikes, 1991), herbivore tooth collagen (Ambrose and DeNiro, 1989), lacustrine pollen (Maitima, 1991), and relatively abundant and well-studied faunal remains (Marean, 1992; Marean et al., 1994). Collectively, these datasets indicate a dry, grassy period ~6.5–4 kya, during which hunter-gatherers may have followed shifting ecotones along the Rift escarpment (Ambrose, 1998). Archaeological contexts are also comparatively well-documented and dated in this area (e.g., Ambrose, 1998). Caprines appear in low numbers at a forager-occupied rockshelter along the escarpment, possibly as early as ~4.9 kya (Ambrose, 1998; Marean, 1992). Specialized pastoralism only flourishes here and in the broader Rift Valley and adjacent plains after ~3.3 kya (Gifford-Gonzalez and Kimengich, 1984; Gifford-Gonzalez, 1998). Expansion of herders may relate to multiple environmental and social factors, including bimodal rainfall seasonality and the possible expansion of grasslands (Marshall, 1990), the ability of herders to manage zoonotic disease risks in these grasslands (Gifford-Gonzalez, 2000), and social responses to increased rainfall unpredictability, including new mobility patterns and social networks (Marshall et al., 2011). Evaluating these possibilities will require additional high-resolution paleoenvironmental data, which can be integrated with local archaeological sequences as we have done here for LTB and LVB.

Future environmental sequences from potential source areas for herding may echo or deviate from patterns seen in LTB and LVB. Within each local sequence, precise relations among environmental, economic, and social changes must be explored with special attention to material cultural indicators of subsistence strategies, mobility patterns, and social interactions instrumental in thwarting or enabling the spread of herding. Crucially, comparing sequences of different areas may elicit causes for patterns of economic change in particular settings.

5.5. Paleoecology and the spread of food production in eastern Africa

The advent of herding in eastern Africa followed distinct trajectories in LTB, LVB, the Central Rift Valley, and adjacent plains, with variations in timing and social context (Marshall et al., 2011;

Lane, 2013). Though our knowledge of early herding around Lake Turkana is based on only a few sites, recent research is deepening our understanding of major social and economic changes ~5–4 kya (Hildebrand et al., 2018). At GaJi2/4, cattle and caprines appear for the first time in eastern Africa, and comprise a substantial portion of the identifiable mammalian assemblage, indicating the immediate importance of herding in this basin (Marshall et al., 1984; Barthelme, 1985). A new ceramic tradition (Nderit pottery) appears at several sites, signaling cultural changes (Hildebrand and Grillo, 2012; Grillo and Hildebrand, 2013). Construction of monumental pillar sites testifies to new mortuary practices involving hundreds of people (Hildebrand et al., 2018).

These socio-economic changes coincide with each other and with dramatic climatic and ecological changes described above, but untangling the exact relations among these changes is tricky. Climatic changes could have operated in a "push" fashion: as Lake Turkana shrank and prime fishing areas disappeared, FGH economies may have become unpredictable. Climate changes also could have created "pull" effects: new plains revealed by Turkana's receding shores may have attracted pastoralists. Finally, uncertainty stemming from the combined effects of changing climates and environments might have led local FGH people and incoming herders to seek closer contact and cooperation. Fishing may have played an important role in the spread of herding: initial spreads of people may have been driven southward by seeking new aquatic resources, settling in lacustrine basins along the way, with herders following afterwards. Many early herding sites also contain evidence of aquatic resource exploitation, suggesting that fishing may have played a role in the spread of early herders.

By contrast, the earliest introduction of livestock to LVB ~4.2–4.0 kya witnesses no dramatic changes in material culture, settlement patterns, or mortuary practices. Small amounts of livestock are integrated into otherwise FHG subsistence economies at Wadh Lang'o (Prendergast, 2010), possibly at Gogo Falls (Karega-Munene, 2002; cf. Robertshaw, 1991), and the Usenge 3 site (Lane et al., 2007). This first appearance of livestock occurs amid material culture continuity: Kansyore ceramic décor shifts only slightly, and lithic raw material choices and manufacture remain unchanged (Dale, 2007; Dale and Ashley, 2010; Seitsonen, 2010). Paleoecological proxies are similarly suggestive of stasis in local environments, and this is corroborated by a lack of change in wild fish and game exploitation (Lane et al., 2007; Prendergast, 2010).

The appearance of Elmenteitan pottery at Wadh Lang'o and Gogo Falls coincides with an increase in caprine and cattle remains. This PN ceramic tradition was already widespread and associated with highly specialized pastoralist economies in the Central Rift Valley and southwestern Kenya as early as ~3 kya (Robertshaw, 1988; Marshall, 1990). Its appearance in LVB is accompanied by shifts in lithic production, including an emphasis on Rift Valley obsidian (Robertshaw, 1991; Seitsonen, 2004). However, unlike their inland counterparts, people around Lake Victoria continued wild fish and game exploitation alongside animal husbandry (Marshall and Stewart, 1995; Prendergast, 2008). Here, possible population shifts, and/or extensive contact with inland pastoralist populations, are more likely causes of material and economic shifts than climatological or ecological factors, especially since proxies continue to indicate ecological stasis.

These two basins for eastern African prehistory display strong environmental, economic, and cultural contrasts. Herding in LTB began alongside novel ceramic production and mortuary practices during an abrupt (<1 kyr) climatic event that shrank Lake Turkana, created vast new plains along retreating lakeshores, and ultimately transformed vegetation, herbivore communities, herbivore diets, and/or human choices in herbivore predation. In contrast, LVB witnessed two relatively muted economic shifts amidst fairly stable ecological conditions: the initial adoption of herding within a long-term local FHG tradition, and the subsequent proliferation of livestock alongside newly-introduced pastoralist material culture, but within a framework of continuing FHG activity. While climatic and/or environmental shifts are likely to be at least partially responsible for social and economic transformations in LTB, social factors seem to be the primary, indeed, perhaps the only, driver of change in LVB.

6. Conclusions

The comprehensive paleoecological dataset presented in this study provides a vital comparative record for two Kenyan lake basins that document separate and distinct stages of the spread of food production in eastern Africa during the Holocene. Nuanced comparisons reveal different ecological responses between basins, and even variable sequences of ecological change within a single basin (LTB). Contrasting information from different proxies should caution researchers against relying on any one proxy from a single locality to provide a comprehensive ecological reconstruction for a region.

Results also reveal complex relations between ecological change and early herding in eastern Africa: in LTB local ecological changes prompted by the end of the AHP coincide with the appearance of herding, whereas in LVB a more gradual introduction of herding occurs amidst relative ecological stasis. A comparison of Turkana and Ele Bor environments in northern Kenya also highlights the unique sensitivity of this basin, relative to inland areas, emphasizing the importance of locally specific proxy studies. Future research should expand to additional inland and source areas, in order to rigorously examine the ties, if any, among climate, ecology, and herder behavior.

Author contributions

Conceived and designed the research: KLC, TEC, KHF, EAH. Performed the research: KLC, AJ. Analyzed the data: KLC, TEC, KHF, EAH. Contributed samples: EAH, AJ, MEP. Provided analytical tools/reagents/materials: TEC, KHF. Wrote the paper: KLC, EAH, AJ, MEP.

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Appendix A. Supplementary data

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